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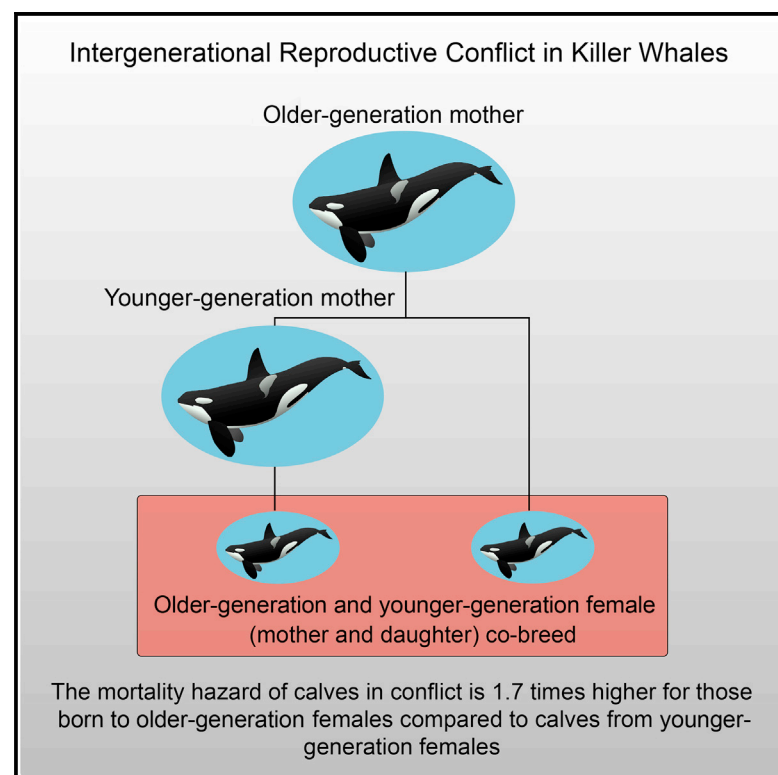
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Current Biology

Reproductive Conflict and the Evolution of Menopause in Killer Whales

Graphical Abstract



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In Brief

Croft et al. show that in resident killer whales, older mothers suffer disproportionate costs when breeding at the same time as their daughters, an effect driven by the unusual demography of resident killer whales. These findings can explain for the first time why reproductive and somatic senescence have been decoupled in resident killer whales.

Highlights

- Local group relatedness increases with age in female killer whales
- Young females are predicted to invest more in reproductive competition
- The costs of co-breeding with kin are greater for old compared to young females



Reproductive Conflict and the Evolution of Menopause in Killer Whales

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SUMMARY

Why females of some species cease ovulation prior to the end of their natural lifespan is a long-standing evolutionary puzzle [1–4]. The fitness benefits of post-reproductive helping could in principle select for menopause [1, 2, 5], but the magnitude of these benefits appears insufficient to explain the timing of menopause [6–8]. Recent theory suggests that the cost of inter-generational reproductive conflict between younger and older females of the same social unit is a critical missing term in classical inclusive fitness calculations (the “reproductive conflict hypothesis” [6, 9]). Using a unique long-term dataset on wild resident killer whales, where females can live decades after their final parturition, we provide the first test of this hypothesis in a non-human animal. First, we confirm previous theoretical predictions that local relatedness increases with female age up to the end of reproduction. Second, we construct a new evolutionary model and show that given these kinship dynamics, selection will favor younger females that invest more in competition, and thus have greater reproductive success, than older females (their mothers) when breeding at the same time. Third, we test this prediction using 43 years of individual-based demographic data in resident killer whales and show that when mothers and daughters co-breed, the mortality hazard of calves from older-generation females is 1.7 times that of calves from younger-generation females. Intergenerational conflict combined with the known benefits conveyed to kin by post-reproductive females can explain why killer whales have evolved the longest post-reproductive lifespan of all non-human animals.

RESULTS AND DISCUSSION

The “reproductive conflict hypothesis” predicts that unusual kinship dynamics in humans, killer whales (*Orcinus orca*), and short-finned pilot whales (*Globicephala macrorhynchus*) have predisposed these species to evolve early reproductive cessation in response to intergenerational reproductive conflict [6, 9]. Kinship dynamics describe the age-related changes in local relatedness that are driven by patterns of mating, dispersal, and mortality [6, 9]. In African apes and, potentially, ancestral humans, female-biased dispersal and local mating within groups is predicted to lead to an increase in female relatedness to local group members with age [9]. As a result, younger females are predicted to invest more in competitive effort in comparison to older females, and older females should suffer disproportionate costs when in reproductive conflict with younger females. In humans, reproductive competition among co-breeders is expected to be particularly intense because of the reliance on food sharing [5, 10]. Under these conditions, theory predicts that females should cease reproduction when females from a younger generation start to reproduce [6]. In contrast to apes and ancestral humans, dispersal is not female biased in menopausal cetaceans. In killer whales, neither sex disperses from the matrilineal group and mating occurs non-locally [11, 12]; evidence suggests that short-finned pilot-whales exhibit a similar social structure [13]. Surprisingly, this other unusual mammalian demographic pattern (the “whale” case) is also predicted to lead to increasing age-specific relatedness of reproductive females to other group members, a pattern driven primarily by increased age-specific relatedness to local males [9]; at the start of her reproductive life, a female’s relatedness to males in her local group is relatively low, because her father is from a different social group. As a female reproduces, her sons will remain in her group, increasing her overall age-specific local relatedness (Figure 1A). While ape-like demography is known to exacerbate the cost of reproductive conflict for older females and favor early cessation of reproduction in humans [6, 14, 15], the consequences of killer whale demography for reproductive conflict are unknown.

First, we determined whether patterns of age-specific relatedness in killer whales fit the pattern of kinship dynamics (i.e., an

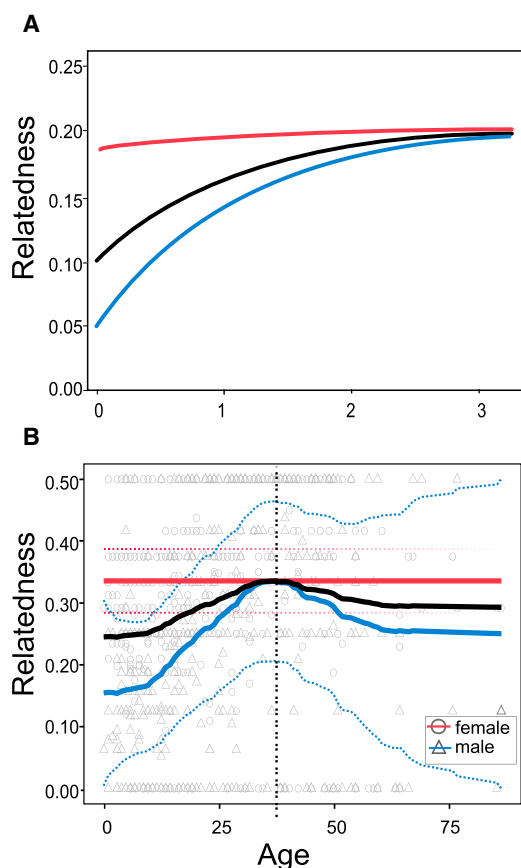


Figure 1. Age Changes in Local Relatedness

(A) Theoretical predicted relationship between female age (scaled relative to mean generation time) and mean relatedness to other females (red line) and males (blue line) within the same matriline taken from the previous model of Johnstone and Cant [9], which assumes no post-reproductive females. Averaged relatedness across both sexes is also shown (black line).

(B) Relationship between female age and maternal relatedness in Northern and Southern resident killer whales (using data from 1980, 1990, and 2000) for a total of 200 whales over 846 whale-years. Lines indicate patterns of relatedness as in (A) (SEs are shown as dotted lines). The raw empirical data are also plotted. Lines are plotted using a local linear trend model. The vertical dotted line indicates the age at which 95% of female lifetime fecundity is completed.

increase in local relatedness with reproductive female age) as predicted by previous theory ([9]; Figure 1A). Second, we developed a new model to investigate the predicted outcome of reproductive conflict given killer whale demography. Finally, we tested our model predictions using over four decades of individual-based demographic data from two resident killer whale populations, which have the longest recorded post-reproductive lifespan of all non-human animals—females generally stop reproducing in their 30s to 40s but can survive into their 90s [16].

Age-Specific Changes in Relatedness in Resident Killer Whales

Using the demographic data from the two populations, we found that the mean relatedness of a female killer whale to her local group (matriline) increases with age during the reproductive period, due to an increase in relatedness to local males (Fig-

ure 1B). In contrast, mean relatedness to local females remains constant with age because females are born into their mother's group and so have a high local relatedness to local females at birth. These findings are in accordance with previous theoretical predictions ([9]; Figure 1A) and closely match observed kinship dynamics in the matrilineal Mosuo of southwestern China among whom, very much like the resident killer whales, brothers and sisters of three generations live together and males do not live with their own offspring [17]. In the resident killer whales, the observed peak in local relatedness of females to their local group (Figure 1B) coincides with the age of reproductive termination in females (95% of lifetime fecundity is completed by age 39), after which local relatedness declines, presumably because post-reproductive females cease to produce new offspring to compensate for the mortality of existing offspring, particularly sons, which often do not survive beyond 30 years (median lifespan of sons that reach sexual maturity = 29 years, 95% confidence interval: 26–32). The model predictions from Johnstone and Cant [9] shown in Figure 1A did not explicitly model the evolution of reproductive cessation itself, assuming instead that fecundity is independent of age. Consequently, while the model (Figure 1A) accurately predicted patterns of local relatedness to males and females up to the point of reproductive cessation, it did not predict the observed decline in relatedness for post-reproductive females (Figure 1B).

Predicting the Consequences of Kinship Dynamics for Reproductive Conflict in Killer Whales

We developed an inclusive fitness model of how kin competition impacts on age-specific changes in female reproductive competitive effort, using an infinite-island structured population framework [18, 19]. An earlier model of this kind showed that killer whale demography (featuring very limited dispersal of both sexes, combined with non-local mating) could give rise to age-specific changes in relatedness favorable to the subsequent evolution of early reproductive cessation ([9]; Figure 1A). As outlined above, however, that model did not explicitly consider the evolution of reproductive cessation itself. Here, we analyze the evolution of differences in reproductive competitive effort between older and younger females in a demographically explicit framework. To incorporate reproductive conflict, we assume that females can selfishly increase their own personal fecundity at a cost to the overall fitness of the group, by investing time and effort in competing for resources and producing their own young. In resident killer whales, such competitive effort by females may reduce the fitness of all group members, both females and males, through its negative impact on food sharing [20], through inter-individual conflicts over collective movement [21], and through reductions in the assistance that mothers are thought to provide to boost their sons' mating success in encounters between groups [22]. To capture the demography seen in resident killer whales [16], male mortality is assumed to be twice that of females (assuming equal mortality does not qualitatively change the predictions of the model). We then examined how different patterns of kinship dynamics affect the stable levels of competitive effort and fecundity of older and younger females.

We show illustrative solutions for three cases: the “typical mammal” case, in which mating is local (within the same group)

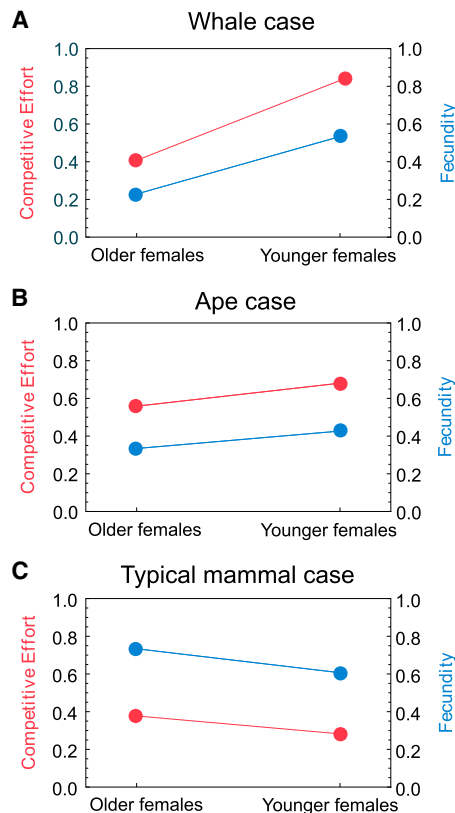


Figure 2. Predicted Levels of Competitive Effort and Fecundity

Predicted levels of competitive effort (red) and fecundity (blue) of older and younger females for three different cases (assuming cost and competition functions detailed in the [Supplemental Experimental Procedures](#)): (A) the “whale” case, (B) the “ape” case, and (C) the “typical mammal” case (see text for details). Axes are scaled such that a mean competitive effort of 1 implies total loss of group fecundity, while a fecundity of 1 corresponds to the value obtained in the absence of any competition.

and only males disperse; the “ape” case, in which mating is local and only females disperse; and the “whale” case, in which mating is non-local and neither sex disperses. The typical qualitative predictions of the model for these three cases are illustrated in [Figure 2](#). In the “typical mammal” case, older females outcompete younger rivals, while in the “ape” and “whale” cases, younger females are predicted to outcompete older rivals. This outcome is a consequence of age-specific increases in relatedness of females to males within their group under the “ape” and “whale” models, which increase the indirect costs of competition and favor lower levels of competitive effort for older compared to younger females. These effects are expected to be particularly strong in humans compared to other primates because of the reliance on food sharing and the provisioning of food by other group members [5, 10]. Intriguingly, the effect is predicted to be even stronger in the “whale” than in the “ape” case ([Figure 2](#)). In both cases, lower competitive effort by older females can translate into greater reproductive output for the rest of the local group. But in the “whale” case, non-local mating means that additional offspring fathered by local males are born outside the group and therefore do not compete with other

related young. Post-reproductive females can therefore maximize inclusive fitness benefits by directing care toward sons [9, 21, 23].

In summary, our model predicts that in resident killer whales, intergenerational reproductive conflict will be costly but younger females will suffer lower costs than older females and gain higher fecundity when in intergenerational reproductive competition. In situations without competition, females are expected to gain higher fecundity than in situations with competition.

Testing for the Effects of Reproductive Conflict in Resident Killer Whales

We tested our model predictions using demographic data from the Northern and Southern resident killer whale populations. The youngest recorded female to have a calf was 9 years old (median age at first birth = 15 years, interquartile range = 15–18 years), and the median calving interval was 6 years (interquartile range = 4–9 years). Females generally stop reproducing in their 30s–40s, and it is common for two generations of females to co-breed in the same matriline (30.7% of calves, 161 of 525 births, were observed to be born into reproductive conflict). We define intergenerational reproductive overlap from the perspective of the older (first)- and younger (second)-generation mother [15]. In the case of the older-generation mother, we define reproductive overlap as when an older-generation female gives birth to a calf within 2 years on either side of the birth of a grand-offspring. In the case of the younger-generation mother, we define reproductive overlap as when a younger-generation female gives birth to a calf within 2 years on either side of the birth of a sibling. Our definition captures the period of time when mothers are in the greatest conflict over resources. Prior to parturition, females need resources to conceive and provision their gestating offspring. Following parturition, killer whales need approximately 42% more food to support lactation [24]. We measured the consequences of reproductive competition for offspring survival to age 15 (the approximate age at which both males and females reach sexual maturity [16]). Although we expect competition to have the greatest impact on offspring survival during lactation, we analyzed survival up to 15 years because competition during these early years may have delayed mortality costs on offspring [15]. For competing offspring, birth order is likely to have a significant effect on survival. Birth order was determined for each calf observed in intergenerational reproductive conflict. We defined birth order by considering all other calves that a calf was in intergenerational conflict with and then determining its position within that cohort.

As predicted by our model ([Figure 2](#)), mothers from the older generation suffered disproportionate fitness costs in reproductive competition with mothers from the younger generation ([Figure 3](#)). Calves from older mothers that were born into situations of reproductive conflict had a 1.67× higher hazard of mortality (when controlling for birth order) than calves that were born from younger-generation mothers in reproductive conflict ([Figure 3](#); [Table S1](#)). The lower survival of calves from older-generation mothers in reproductive conflict cannot be explained due to a general effect of mother’s age on offspring survival, as we found no effect of mother’s age on offspring survival to age 15 across all calves born during the study period (including

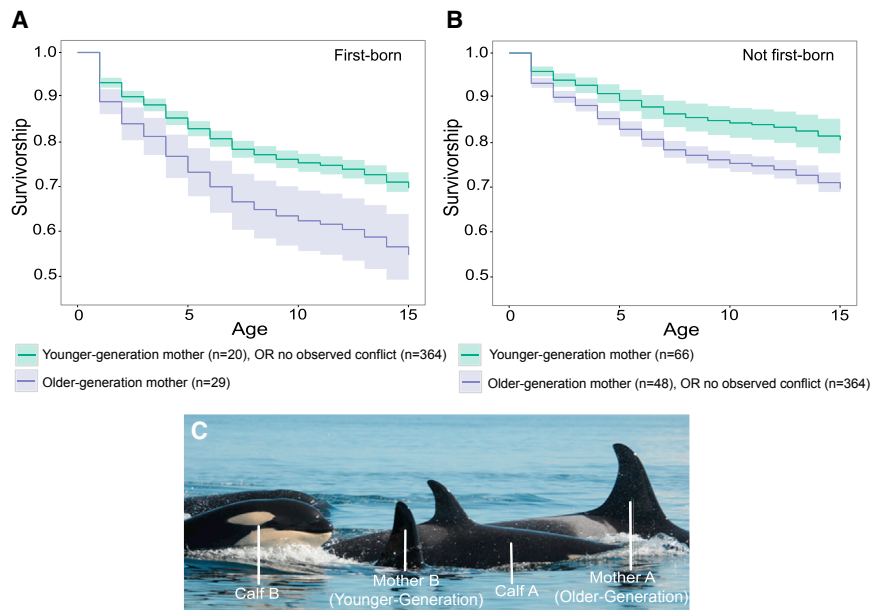


Figure 3. The Effect of Reproductive Conflict in Resident Killer Whales

(A and B) Survival curves (\pm SE) obtained using the model $h(t) = h_0(t) \exp\{\beta_1(G_O + B_O + G_N)\}$ with imputation for missing covariates ($p = 0.005$). All data were analyzed together, but for clarity we report the survival curves in two panels: (A) calves born first in reproductive conflict, and (B) calves not born first in reproductive conflict. For comparison, we also show the survival curves of calves born with no observed reproductive conflict, which by definition do not have a birth order.

(C) An example of reproductive conflict: older-generation mother (mother A) has a calf (calf A) within 2 years of her adult daughter (mother B) having a calf (calf B).

See also [Figure S1](#) for survival curves for the observed data and [Table S1](#) for model fitting results.

calves born in and out of reproductive conflict; Cox proportional hazards, $N = 525$, hazard ratio = 1.0083, $z = 0.56$, $p = 0.59$).

As in humans [25], a major factor driving reproductive conflict in resident killer whales is likely to be their reliance on food sharing, which is a fundamental component of their foraging behavior [20]. Resident killer whales forage in social groups and feed almost exclusively on salmon during the summer months [26], and individual salmon are often shared with other group members [20]. Annual variation in salmon abundance is an important driver of both reproductive success and mortality in resident killer whales [27, 28], highlighting the potential for competition and conflict over access to food. This, combined with the fact that offspring are dependent for many years on the care of their mothers [16, 23], means that reproduction by older females is likely to come at a substantial cost to other group members.

In addition to calves from older mothers suffering a higher hazard of mortality when in reproductive conflict, birth order significantly affected calf survival, with calves born first in reproductive conflict having a 1.95 \times higher hazard of mortality than later-born calves in reproductive conflict (Figures 3A and 3B; Cox proportional hazards, $N = 161$, hazard ratio = 1.94895, $z = 1.99$, $p = 0.046$). We suggest that the survival advantage of the calves born into a group that already has another calf could arise through the benefits of alloparental care, such as babysitting, or allosuckling. In these instances, calves born into a group with another lactating mother may benefit from enhanced alloparental care during the first year of life. In contrast, first-born calves may experience the first year of life without another lactating female in the group and thus may not benefit from the same level of alloparental care during early life, when mortality is high [29].

In contrast to our prediction that in situations without competition females would gain higher fecundity than in situations with competition, calves of younger-generation mothers that were not first-born in reproductive conflict had higher survival than

calves born into situations where there was no observed conflict (Figure 3B).

This effect may be driven by “grand-mother benefits,” such as the benefits of leadership during periods of food scarcity [21]. By default, the grandmothers of calves of younger-generation mothers that are born into reproductive conflict will be alive at the time of conflict (as they have also given birth). In contrast, many calves born into the no-observed-conflict group will be born in instances where the grandmother is no longer alive. It is also possible that young females gain benefits as a result of co-breeding with their mother (e.g., due to the benefits of allosuckling). From an evolutionary perspective, however, the direct fitness costs of reproductive conflict to older-generation females (increased mortality hazard of their own calves) are substantially greater than the indirect benefits of co-breeding (increased survival of grand-offspring).

Non-human species that exhibit prolonged post-reproductive lifespans provide a rare opportunity to test the assumptions and predictions of theoretical models for the evolution of menopause in populations with natural fertility and mortality. Previous work in resident killer whales has shown that post-reproductive females increase the survival of their adult offspring, particularly their adult sons [23], by transferring knowledge of when and where to find salmon [21]. Such benefits however, cannot explain why females stop reproduction midway through their life. Indeed, in other long-lived social mammals such as elephants (*Elephas maximus* and *Loxodonta africana*), old females confer survival benefits to their kin, including their grand-offspring [30–32]. In elephants, however, females typically maintain reproductive capability until the end of life [33, 34]. Our new findings highlight the unusual demography of killer whales and the consequences of this demography for intergenerational reproductive conflict as a key mechanism selecting for early reproductive cessation. This is in contrast to the majority of cooperative breeding vertebrates, in which patterns of demography select for older females to invest more in competitive effort in comparison to younger females, often leading to the reproductive suppression of younger females [35–37]. More generally, our study supports the contention [9] that inclusive fitness models incorporating both the

inclusive fitness costs of reproductive conflict and the inclusive fitness benefits of late-life helping (grandmother and mother benefits) may explain why, of all long-lived social mammals, prolonged post-reproductive life appears to have evolved only in humans and toothed whales.

EXPERIMENTAL PROCEDURES

Study Populations

Demographic records were collected annually (1973–2015) using photographic censuses for two resident killer whale populations: the Southern and Northern populations in inshore coastal waters off Washington State, USA, and British Columbia, Canada (see [16, 29] for details). Resident killer whales are typically observed between May and November, when the animals frequent the inshore waters [29]. Individuals were identified by their unique fin shapes, saddle patches, and the presence of any nicks or scratches and were sexed using distinctive pigmentation patterns around the genital slits.

We censored the data to include only reproductive events that occurred during the study period (1973–2015). Genealogical relationships were inferred from long-term observations of social organization [11, 38] and mothers were identified by association with young calves [39]. During the 43 years of data collection, 525 calves (111 females, 124 males, 290 unknown sex) were recruited to the study populations from known mothers and were aged in reference to their year of birth. As there is no dispersal from either population [16], mortality was recorded if an individual's matriline was observed in the population within a given year but the individual did not appear. During the study period, 137 individuals with known mothers died in the first 15 years of life. Of the 525 calves recruited to the population, 161 were involved in intergenerational reproductive conflict, and 364 calves were not involved in any observed reproductive conflict. Because calves are typically first sighted when they are 6 months old [29], neonate deaths will be under-recorded. As a consequence, calves that we classify as having no observed reproductive conflict could have experienced a very short period of reproductive conflict (because a competitor calf died before it was observed). The under-recording of neonate deaths will mean that we will underestimate true calf mortality and that our analysis of the effect of reproductive conflict on calf survival is thus conservative.

Modeling the Consequences of Kinship Dynamics for Reproductive Conflict in Social Mammals

To determine the evolutionarily stable levels of competitive effort for females of different age ranks, we adopt an adaptive dynamic approach, assuming that evolution proceeds by the successive substitution of mutations of small effect, with a clear separation of timescales between demographic and evolutionary processes. We consider a population comprising a very large number of discrete groups, each of which contains n breeding individuals of each sex (for a total of $2n$ individuals per group) that can be ranked by age. Given that almost all cases of reproductive conflict in our population involve females from two generations, we focus on the case in which $n = 2$ (larger group sizes yield qualitatively similar results). We model the demographics of this population in continuous time. Individuals of sex $s \in \{f, m\}$ and age rank a within their group experience mortality rate μ_{sa} . An individual who dies is immediately replaced by a juvenile of the same sex who might be either locally born or immigrant (and locally or non-locally sired). The probability that a successful offspring of sex s is produced by any given female is proportional to her fecundity multiplied by a weighting factor of h_s for local females, and $(1 - h_s)$ for non-local females, such that h_s specifies the probability of replacement by a philopatric offspring of sex s . Similarly, the probability that the offspring was sired by any given male is proportional to his mating output, multiplied by a weighting factor of l for local males in the same group as the mother, and $(1 - l)$ for non-local males, such that l specifies the probability that an offspring is the product of a local mating.

Females of age rank a invest some level of effort x_a in competition over reproduction. Total female fecundity and male mating output within the group are decreasing functions of total competitive effort ($\sum_a x_a$), while a female's share of that total is an increasing function of her individual effort relative to

the mean effort of her competitors ($x_i - 1/n - 1 \sum_{j \neq i} x_j$). For any given vector of age-rank-specific competitive effort levels x , we determine the coefficients of relatedness between individuals of different sexes and age ranks at demographic equilibrium, as well as the reproductive values of individuals of different sexes and age ranks (as detailed in the Supplemental Information). We then use these to determine the selection gradient acting on each competitive effort level, i.e., the slope of fitness with respect to competitive effort for a mutant allele (of small effect) that affects the behavior of females of that particular age rank (as detailed in the Supplemental Information). Repeated updating of the vector of competitive effort levels x by addition of the vector of selection gradients leads ultimately to a convergently stable equilibrium at which all selection gradients are equal to zero, which we take as the solution of the model.

The quantitative predictions of the model are sensitive to the precise form of these functions; we focus therefore on qualitative predictions that hold for a range of different functional forms. We show illustrative solutions for three cases: the “typical mammal” case, in which mating is local and only males disperse ($m = 1$; $h_f = 1$, $h_m = 0$); the “ape” case, in which mating is local and only females disperse ($m = 1$; $h_f = 0$, $h_m = 1$); and the “whale” case, in which mating is non-local and neither sex of young disperses ($m = 0$; $h_f = 1$, $h_m = 1$).

Testing for the Effects of Reproductive Conflict in Resident Killer Whales

To determine the effects of reproductive conflict on offspring survival, we fit a Cox proportional hazards model to the demographic killer whale dataset. We do not consider intergenerational conflict across three or more generations, which occurs infrequently in the study populations. For some whales ($n = 51$), birth order could not be determined because two or more offspring in conflict were born within the same year and the resolution of the data is such that it is not possible to determine birth order within a year. It is well known that eliminating data due to incomplete covariate information is likely to produced biased results [40]. We run a Monte Carlo simulation with 10,000 replications in which we simulate birth order of calves born in conflict in the same year, assigning equal probability to each possible birth order. We confirmed that our data met the assumption of proportional hazards (goodness-of-fit testing approach on the Schoenfeld residuals, $H_0 = PH$, $\chi^2 = 0.66$ $p = 0.43$).

We fitted a Cox proportional hazards model with the following possible indicator covariates:

- $G_O = 1$ if older generation in conflict
- $G_Y = 1$ if younger generation in conflict
- $G_C = 1$ if in conflict
- $G_N = 1$ if not in conflict
- $B_O = 1$ if oldest calf in conflict cohort (i.e., born earliest)
- $B_{no} = 1$ if not oldest calf in conflict cohort (i.e., not born earliest)

Both birth order and conflict type had clear and overlapping effects on a calf's survival probability (Figure S1). We therefore combined birth order and conflict type covariates into a model in interacting and non-interacting configurations. We then used an Akaike information criterion (AIC) to select the most parsimonious model (Table S1). The most parsimonious and best-fitting model was $h(t) = h_0(t) \exp\{\beta_1(G_O + B_O + G_N)\}$, (AIC = 1630.6, $p = 0.005$), in which calves of younger-generation females born first into reproductive conflict, calves from older-generation females not born first into reproductive conflict, and no observed conflict calves had the same hazard. The predicted survival curves from the final model are shown in Figure 3.

SUPPLEMENTAL INFORMATION

Supplemental Information includes one figure, one table, and Supplemental Experimental Procedures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.12.015>.

AUTHOR CONTRIBUTIONS

D.P.C., M.A.C., and D.W.F. conceived the project, which was coordinated by D.P.C. R.A.J. and M.A.C. wrote the theoretical model. Field data were

collected by K.C.B. and J.K.B.F. S.E. and S.N. carried out the survival analysis with input from S.M., L.J.N.B., D.W.F., and D.P.C. D.P.C., S.E., R.A.J., and L.J.N.B. prepared the figures. D.P.C., M.A.C., and R.A.J. drafted the manuscript with input from all authors.

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